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Phenolic content and palatability of leaves and wood to soil isopods and diplopods

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With 3 figures

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1. Introduction

The role of millipedes and isopods in soil litter degradation has received little study in North America, most of the work having been done in Europe (EDWARDS 1974). There is very little information on the food preferences of isopods. Millipedes prefer certain species of leaves (LYFORD 1943; DUNGER 1962), and both isopods and millipedes prefer weathered litter to freshly fallen leaves and wood (EDWARDS 1974; VAN DER DRIFT 1951).

In this study we examined the leaf feeding preferences of 25 species of leaves to 4 species of diplopods, *Narceus americanus* (BEAUVOIS), *Diploiuulus* sp., *Pseudopolydesmus serratus* (SAY), *Apheloria coriacea* (KOCH), and 4 species of isopods, *Oniscus asellus* L., *Armadillidium vulgare* (LATREILLE), *Armadillidium nasatum* BUDDÉ-LIND, and *Porcellio scaber* LATREILLE. We also tested 3 species of diplopods, *N. americanus*, *P. serratus*, and *Oxidus gracilis* (KOCH), and 3 isopods, *O. asellus*, *A. vulgare*, and *A. nasatum* to determine at what point in the process of fungal decay certain wood species become ingestible, and whether one of these animal taxa is more inclined than the other to consume edible samples of very heavily decayed wood. In addition, since EDWARDS (1974) suggested that one of the main factors influencing palatability seems to be the "sort and amounts of polyphenols in the litter", we inquired into this possibility. We also examined the possibility of a correlation between leaf preference and the content of water soluble extractives in the leaves, suspecting that perhaps these extractives, unlike insoluble high molecular weight compounds, would possess certain chemotropic or nutritive characteristics. Finally, we analyzed the edible wood samples for total phenolic content, percentage of water soluble extractives, lignin content, and reducing sugars to determine whether one or more of these factors was correlated with the quantity of wood consumed.

2. Methods

Animals were collected from a woodlot near the College and were stored at 15 °C until needed. Leaves were collected immediately after falling in October and November 1974; they were air dried and stored in plastic bags at 22 °C until needed. All leaf feeding experiments were concluded within seven months of leaf fall. Undecayed wood was obtained from the Wood Products Engineering Department at the College. Decayed wood was obtained from a nearby woodlot. This wood, referred to in this paper as "woodlot wood", was dried at room temperature and stored at 22 °C until needed. The leaf experiments were based on an incomplete random block design of lattice squares as shown in Figure 1 (DAVIES 1963). The 25 species of leaves were assigned positions A to Y using a random numbers table (STEELE and TORRIE 1960). All 10 runs were replicated twice for each invertebrate species and the data were analyzed through stepwise regression.

Each leaf feeding run was carried out in a culture dish 8 cm high and 18 cm diameter containing 300 g sand and 65 ml water. A floor of wire screen was divided into 5 equal parts using rubber insulated 14-gauge wire held in place by 2 pieces of bare copper wire. The screen was suspended

Run	Leaf Species				
1	A	B	C	D	E
2	F	G	H	I	J
3	K	L	M	N	O
4	P	Q	R	S	T
5	U	V	W	X	Y
6	A	F	K	P	U
7	B	G	L	Q	V
8	C	H	M	R	W
9	D	I	N	S	X
10	E	J	O	T	Y

Fig. 1. Lattice square experimental design, with letters representing leaf species.

about 5 mm above the sand by a pliant caulking compound which was also used to seal the upper perimeter of the screen against the wall of the glass dish. This setup provided the animals with a moisture-saturated atmosphere and free access to the 5 leaf species presented during each run. The wire screen allowed the feces to fall into the sand below, thus minimizing the chances of coprophagy.

The leaves were dried at 105 °C for 24 hours. Weighed quantities of 5 species were placed separately in the 5 sections of a culture dish. Fifteen specimens of each isopod species, 10 *Diploiuulus* sp., 10 *P. serratus*, 5 *N. americanus* and 5 *A. coriacea* were used in each run. Feeding was allowed to proceed at 15 °C in the dark for 1 week. Mortality was then noted and the unconsumed leaf residues were oven dried and weighed. The difference between the initial and final weight of leaves was expressed as mg of leaf eaten per g invertebrate per day.

The water extractable fraction of the leaves was determined by weight-difference. Wiley-milled 20 mesh particles were dried at 105 °C, weighed, extracted with water in a Soxhlet extractor for 4 h, dried at 105 °C, and weighed.

A vanillin (SWAIN and HILLIS 1959), Folin (LOWRY et al. 1951) and 4-amino phenazone procedure (BARUAH and SWAIN 1957) were used for measuring phenolic content in the leaves. The vanillin procedure estimates 1, 3 and 1, 3, 5 phenols. The Folin and 4-aminophenazone procedures estimate the total free phenolic content of the leaves. These assays do not measure methoxyl groups or polymerized phenolics. Phloroglucinol was used to determine the upper limit of linearity between optical density and concentration for each of the procedures. Thereafter, in measuring the quantity of unknowns, extinction coefficients of 28,000, 20,000 and 2,800 were used respectively for the vanillin, Folin and 4-aminophenazone procedures. These coefficients are averages based on 21, 21 and 14 different phenolic compounds (SWAIN and GOLDSTEIN 1964). A molecular weight of 200 was used arbitrarily, and the data were calculated as µg phenolic per 10 mg dry wt leaf tissue.

Tests were also run to determine whether *O. asellus* feeding on leaves of *B. alleghaniensis*, *A. altissima* and *S. nigra*, and *P. serratus* feeding on leaves of *B. alleghaniensis*, were able to catabolize leaf phenolics. The phenolic content of the leaves and feces was measured and an analysis was made of the differences resulting from digestion and absorption.

Blocks of undecayed lumber, cut into 2 cm cubes, were inoculated with brown rot or white rot fungi. *Quercus rubra*, *Ulmus americana*, *Acer saccharum*, and *Tilia americana* L. were inoculated with the white rot *Polyporus versicolor* L. ex FR. and the brown rot *Lenzites trabea* PER. ex FR. *Pinus resinosa* AIR. and *Picea glauca* (MOENCH) VOSS were inoculated with the white rot *Fomes pini* (FR.) KARST and the brown rot *Lenzites trabea*.

50 ml of 1.5% agar and 2.5% malt extract was placed in 6×6×14 cm French square jars. Each jar was inoculated in three places with the desired fungus. V-shaped glass rods were placed over each zone of growth after 3 weeks and three sterilized pre-weighed blocks of wood were placed on the glass rods. After periods of 3, 6 and 12 weeks, the blocks were removed, oven dried, weighed, and used in feeding trials. These wood samples are referred to as "laboratory decayed wood".

The heavily decayed woodlot wood was oven dried, weighed, and presented to invertebrates in the dishes described for the leaf feeding experiments. Five *N. americanus* and 15 *P. serratus*, *O. gracilis*, *O. asellus*, *A. vulgare* and *A. nasatum* were used in each feeding trial. The trials were held at 15 °C for one week. Mortality was noted after each trial, and food consumption was measured and expressed as mg per g invertebrate per day. The phenolic and water extractable contents of the wood were estimated as described above. The lignin content was estimated according to JOHNSON et al. (1961), and reducing sugars according to NELSON (1957).

3. Results

3.1. Mortality

Mortality was very low in all experiments, averaging 1.9% for isopods and 2.0% for millipedes in the leaf feeding experiments and 4.7% for both the isopods and millipedes in the wood feeding experiments.

3.2. Leaf preferences

In general, the isopods and millipedes avoided *A. saccharum* and *A. rubrum*, species of Fagaceae (*Quercus* spp. and *F. grandifolia*), and about half of the gymnosperm species (Table 1). Some species of leaves were avoided by one animal taxon but not the other. *C. cordiformis*, for example, was sparsely consumed by millipedes, but readily so by isopods. Based on the top 5 preferred species of leaves, isopods consumed a greater quantity per unit body weight ($\bar{x}$ 14.62 mg/g/day) than millipedes ($\bar{x}$ 3.31 mg/g/day). Results of the stepwise regression analysis of the leaf preferences are shown in Table 2. The preferences of all of the isopods and two millipedes (*Diploiuulus* sp. and *P. serratus*) are significant for at least five leaf species, while the preferences of the millipedes *A. coriacea* and *N. americanus* are significant for three and four species respectively.

Table 1. Consumption of fallen leaves by soil isopods and diplopods

Leaves	Invertebrates									
	<i>Narceus americanus</i>	<i>Diploiuulus</i> sp.	<i>Pseudopolydesmus serratus</i>	<i>Apheloria coriacea</i>	$\bar{x}$ mg eaten/g/day (millipedes)	<i>Oniscus asellus</i>	<i>Armadillidium vulgare</i>	<i>Armadillidium nasatum</i>	<i>Porcellio scaber</i>	$\bar{x}$ mg eaten/g/day (isopods)
<i>Abies concolor</i> (GORD et GLEND)	0.28	0.29	0.45	0.49	0.37	0.87	0.25	0.84	0.69	0.66
<i>Acer negundo</i> L.	0.57	6.63	2.82	0.79	2.70	9.54	7.20	13.95	24.27	13.74
<i>Acer platanoides</i> L.	0.45	1.11	2.48	0.15	1.04	5.57	2.94	8.67	6.74	5.98
<i>Acer rubrum</i> L.	0.43	1.51	0.65	0.65	0.81	0.22	0.39	0.72	2.47	0.95
<i>Acer saccharum</i> MARSH.	0.45	0.94	0.13	0.34	0.46	2.77	0.08	1.50	2.33	1.67
<i>Ailanthus altissima</i> (MILL.) SWINGLE	6.16	8.34	2.28	0.50	4.31	13.49	8.71	17.91	24.45	16.14
<i>Betula alleghaniensis</i> BRITTON	3.97	8.62	1.93	2.36	4.22	15.04	9.69	22.99	21.50	17.30
<i>Carya cordiformis</i> (WANG) K. KOCH	0.27	1.30	0.52	0.58	0.66	14.88	2.03	8.07	5.18	7.54
<i>Celtis occidentalis</i> L.	0.89	3.88	1.14	0.60	1.62	2.67	4.10	7.30	5.16	4.80
<i>Cornus florida</i> L.	1.30	1.56	0.46	0.44	0.94	6.28	1.19	9.06	6.15	5.67
<i>Fagus grandifolia</i> EHRLH.	0.59	1.50	0.74	1.11	0.98	2.49	0.43	2.26	3.98	2.29
<i>Ginkgo biloba</i> L.	0.24	2.50	0.57	0.50	0.95	1.08	1.58	3.29	3.28	2.30
<i>Liriodendron tulipifera</i> L.	1.35	3.99	1.14	1.70	2.04	5.02	1.43	4.58	9.47	5.12
<i>Picea abies</i> (L.) KARST	0.48	1.41	0.53	0.30	0.68	2.07	1.65	2.78	6.44	3.23
<i>Pinus strobus</i> L.	0.19	0.38	0.49	0.11	0.29	0.31	0.72	0.97	2.07	1.01
<i>Platanus occidentalis</i> L.	1.29	1.25	0.45	0.23	0.80	1.98	1.31	2.73	9.90	3.98
<i>Prunus serotina</i> EHRLH.	0.92	3.65	1.94	0.45	1.74	2.93	1.32	7.16	5.40	4.20
<i>Pseudotsuga menziesii</i> (MIRB.) FRANCO	1.40	2.98	0.81	0.23	1.35	3.53	4.73	7.02	4.24	4.88
<i>Quercus alba</i> L.	0.27	0.25	0.14	0.17	0.21	0.27	0.22	1.12	1.36	0.74
<i>Quercus rubra</i> L.	0.07	0.32	0.13	0.13	0.16	0.11	0.27	0.30	0.88	0.39
<i>Salix nigra</i> M.	2.41	4.92	2.87	0.81	2.75	13.94	11.08	25.94	11.88	15.71
<i>Taxus brevifolia</i> NUTT.	1.15	3.37	0.54	1.28	1.58	4.85	1.00	4.65	6.62	4.28
<i>Thuja occidentalis</i> L.	0.68	0.82	0.42	0.21	0.53	0.67	0.29	1.47	0.75	0.79
<i>Tsuga canadensis</i> (L.) CARR.	0.60	0.89	0.98	0.10	0.64	4.10	1.59	7.05	11.36	6.02
<i>Ulmus americana</i> L.	0.84	1.87	1.12	0.12	0.98	3.45	2.35	10.09	2.83	4.68

Data are mean mg leaf/g invertebrate/day for four separate runs of each invertebrate species.

Table 2. Mean consumption, in mg leaf/g invertebrate/day, for the top five preferred leaf species

Leaves	Invertebrates							
	<i>Nareus americanus</i>	<i>Diploilulus</i> sp.	<i>Pseudopolydesmus serratus</i>	<i>Apheloria coriacea</i>	<i>Oniscus asellus</i>	<i>Armadillidium vulgare</i>	<i>Armadillidium nasatum</i>	<i>Porcellio scaber</i>
<i>Betula</i>	3.97	8.62	1.93	2.36	15.04	9.69	22.99	21.50
<i>allegahaniensis</i>	36.64	18.00	22.69	23.24	17.20	19.68	25.08	23.22
<i>Ailanthus</i>	6.15	8.34	2.28	—	13.49	8.71	17.91	24.45
<i>altissima</i>	71.68	22.07	14.89	—	33.78	19.48	15.88	18.19
<i>Salix nigra</i>	2.41	4.92	2.87	—	13.94	11.08	25.94	11.88
	11.00	7.08	7.94	—	25.08	21.19	25.62	4.16
<i>Acer negunda</i>	—	6.63	2.82	0.79*)	9.54	7.20	13.95	24.27
	—	14.08	12.87	1.98	17.08	15.01	9.07	23.90
<i>Liriodendron tulipifera</i>	—	3.99	1.14	1.70	—	—	—	—
	—	4.19	4.46	11.72	—	—	—	—
<i>Carya cordiformis</i>	—	—	—	—	14.88	—	—	—
	—	—	—	—	22.02	—	—	—
<i>Pseudotsuga menziesii</i>	1.40	—	—	—	—	4.73	—	—
	5.14	—	—	—	—	7.21	—	—
<i>Taxus brevifolia</i>	—	—	—	1.28	—	—	—	—
	—	—	—	7.78	—	—	—	—
<i>Ulmus americana</i>	—	—	—	—	—	—	10.09	—
	—	—	—	—	—	—	4.03	—
<i>Cornus florida</i>	1.30*)	—	—	—	—	—	—	—
	2.10	—	—	—	—	—	—	—
<i>Tsuga canadensis</i>	—	—	—	—	—	—	—	11.36
	—	—	—	—	—	—	—	4.04

*) Significance at 0.10 level; all others significant at 0.01 level.

Note. — The numbers in italics are the F values for each variable.

Table 3. Rank order of top five leaves consumed, using a system of giving the most preferred species a value of 5, and the least preferred a value of 1

Leaves	Invertebrates								
	<i>Nareus americanus</i>	<i>Diploilulus</i> sp.	<i>Pseudopolydesmus serratus</i>	<i>Apheloria coriacea</i>	<i>Oniscus asellus</i>	<i>Armadillidium vulgare</i>	<i>Armadillidium nasatum</i>	<i>Porcellio asellus</i>	Totals
<i>Betula alleghaniensis</i>	4	5	5	5	5	4	4	3	35
<i>Ailanthus altissima</i>	5	4	3	—	2	3	3	5	25
<i>Salix nigra</i>	3	2	2	—	3	5	5	2	22
<i>Acer negundo</i>	—	3	4	2*)	1	2	2	4	18
<i>Liriodendron tulipifera</i>	—	1	1	4	—	—	—	—	6
<i>Carya cordiformis</i>	—	—	—	—	4	—	—	—	4
<i>Pseudotsuga menziesii</i>	2	—	—	—	—	1	—	—	3
<i>Taxus brevifolia</i>	—	—	—	3	—	—	—	—	3
<i>Ulmus americana</i>	—	—	—	—	—	—	1	—	1
<i>Cornus florida</i>	1*)	—	—	—	—	—	—	—	1
<i>Tsuga canadensis</i>	—	—	—	—	—	—	1	—	1

*) Significance at 0.10 level; all others significant at 0.01 level.

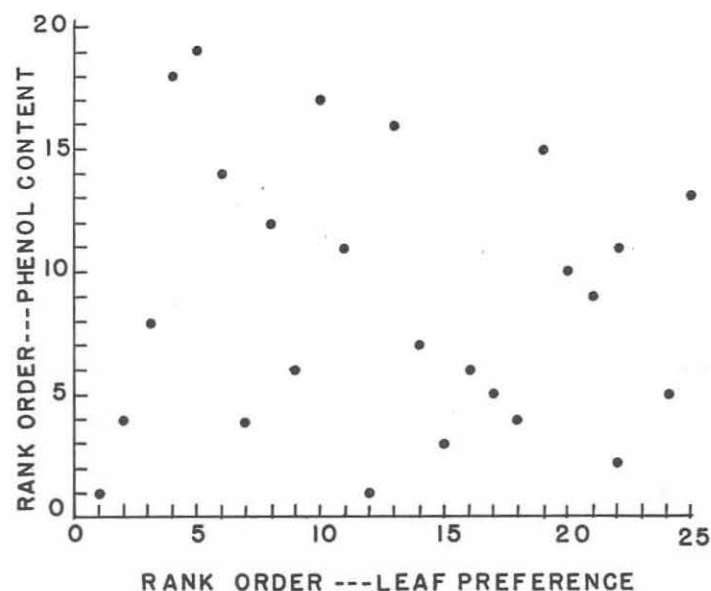


Fig. 2. Rank order plot of leaf preference to isopods against rank order of leaf phenolic content.

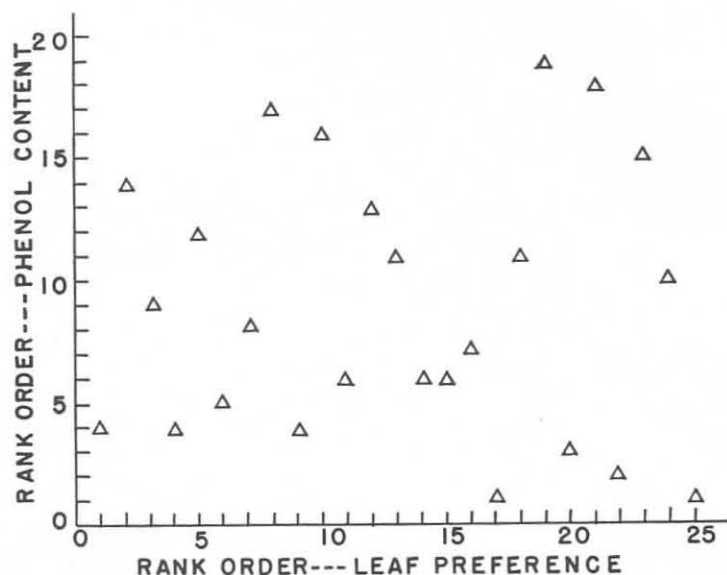


Fig. 3. Rank order plot of leaf preference to diplopods against rank order of leaf phenolic content.

Table 3 shows that four species of leaves were preferred above all others. *B. allegheniensis*, was the favorite, being preferred to all others by half of the animals tested. *A. altissima*, *S. nigra*, and *A. negundo* were also heavily consumed by all of the invertebrates, while *L. tulipifera* was one of the top five favorites for three of the four millipedes. The remaining leaf species were not consistently favored by all of the invertebrates.

3.3. Correlation of leaf preference to phenolics and water extractable content

The tests for phenolics showed no correlation between palatability of leaves (Table 1) and total phenolic content (Table 4) for isopods (Fig. 2) and millipedes (Fig. 3). Thus, *B. allegheniensis* and *A. negundo*, the most highly preferred leaves, fell into the lowest third of the group with regard to phenolic content, while *A. altissima*, *S. nigra* and *L. tulipifera*, which ranked third, fourth and fifth in overall preference, fell into the upper half, but not upper fourth, of the group (Tables 1 and 4).

The weight of the water extractable fraction of the leaves is given in Table 4. No correlation was found between this parameter and leaf preference. Four of the five most-preferred

Table 4. Amount of phenolics present in the leaves tested in μg of phenolics/10 mg leaf

Leaves	Vanillin Assay (1, 3; 1, 3, 5 phenols)	Folin Assay (total phenols)	4-Amino- Assay (total phenols)	Rank order for mean phenols	Water extractable material, % by weight
<i>Abies concolor</i>	22 8	108	132	1 T*)	11.1 10
<i>Acer negundo</i>	23 9	148	186	4 T	16.2 17
<i>Acer platanoides</i>	40 17	232	342	8	13.8 13
<i>Acer rubrum</i>	105 24	912	666	18	26.7 24
<i>Acer saccharum</i>	107 25	888	1,170	19	27.8 25
<i>Ailanthus altissima</i>	46 18	276	600	14	22.4 21
<i>Betula alleghaniensis</i>	20 6	132	252	4 T	16.3 18
<i>Carya cordiformis</i>	36 13	272	420	12	13.0 11
<i>Celtis occidentalis</i>	20 5	204	258	6 T	22.6 22
<i>Cornus florida</i>	33 12	500	672	17	21.1 20
<i>Fagus grandifolia</i>	66 21	256	402	11 T	10.8 9
<i>Ginkgo biloba</i>	19 4	116	108	1 T	14.5 15
<i>Liriodendron tulipifera</i>	87 23	360	678	16	25.8 23
<i>Picea abies</i>	54 20	192	312	7	7.3 2
<i>Pinus strobus</i>	36 14	144	174	3	6.6 1
<i>Platanus occidentalis</i>	37 15	164	312	6 T	9.6 6
<i>Prunus serotina</i>	22 7	168	294	6 T	13.7 12
<i>Pseudotsuga menziesii</i>	18 2	136	216	4 T	10.0 8
<i>Quercus alba</i>	78 22	396	582	15	15.9 16
<i>Quercus rubra</i>	30 11	224	426	10	7.4 3
<i>Salix nigra</i>	39 16	240	390	9	8.6 4
<i>Taxus brevifolia</i>	49 19	240	408	11 T	16.4 19
<i>Thuja occidentalis</i>	29 10	104	186	2	8.7 5
<i>Tsuga canadensis</i>	8 1	152	282	5	13.9 14
<i>Ulmus americana</i>	19 3	276	498	13	9.9 7

*) T indicates a tie in rank-order.

The numbers in bold indicate rank order.

Table 5. Index*) of assimilation of phenolic compounds from freshly fallen decayed leaves in *Oniscus asellus* and *Pseudopolydesmus serratus*

Invertebrate	Leaf Species		μg phenolics/10 mg material		
			Vanillin	Folin	4-amino-phenazone
<i>O. asellus</i>	<i>Betula alleghaniensis</i>	leaves	19.4	49.2	133.8
		feces	16.0	28.4	102.0
		diff. *)	3.4	20.8	31.8
	<i>Ailanthus altissima</i>	leaves	33.0	171.6	278.4
		feces	17.0	104.0	129.6
		diff.	16.0	67.6	148.8
	<i>Salix nigra</i>	leaves	24.4	78.0	88.8
		feces	17.0	52.0	70.2
		diff.	7.4	26.0	18.6
<i>P. serratus</i>	<i>Betula alleghaniensis</i>	leaves	29.0	119.6	146.4
		feces	20.4	93.6	106.2
		diff.	8.6	26.0	40.2

*) A decrement (difference) in phenolic content between leaves and feces can only serve as an index to the quantity of phenolics assimilated.

leaves had high amounts of water extractable materials, but *S. nigra*, the fourth most preferred, ranked in the lowest fifth with regard to water extractability. A double rank-order plot of leaf preference versus water soluble content yielded similar scatter diagrams to those shown in Figures 2 and 3 for leaf preference versus phenolic content.

In some cases large extraction differences were noted between closely related plant species. *Q. rubrum* had half as much water soluble material as *Q. alba*, while *A. saccharum* had twice as much as *A. platanoides*. The significance of this observation is not known.

3.4. Assimilation of phenolics

Table 5 provides data on the phenolic content of leaves and feces based on three assay procedures. The chemical composition of leaf material doubtlessly changes in the course of digestion; certain animal constituents are added to the feces and certain substances are assimilated from the food passageways. Since the nature of these changes is unknown, it is not valid to compare the phenolic content of feces directly with the phenolic content of leaves. It can be presumed, however, that a decrease in percentage of phenols in feces may serve as an index or sign of assimilation. Despite these reservations, it is significant that there was a considerable decrease in phenolic content of feces in comparison to leaves in each of the test situations. The decrease may have been due to microorganisms that reside in the invertebrates. It may have been due also to microbes that are taken into the animal and/or eliminated from the animal with the feces. Regardless of interpretation, large differences are notable between leaves and feces. Reductions upward to about 50 % are seen in some cases for the isopods and 30 % for the millipede.

3.5. Wood feeding

Table 6 shows the percentage weight loss of 6 species of wood exposed to 3 species of fungus. Despite severe losses in some cases (e.g., 37 % of *A. saccharum*), none of these "artificially" decayed materials was suitable for ingestion. The "naturally" decayed woodlot wood, however, was readily consumed (Table 7). In this table and succeeding tables dark and light refer to the coloration of the decayed woodlot wood.

3.6. Wood analyses

Table 8 shows the chemical data that were obtained for the five specimens of woodlot wood.

Table 6. Percent weight loss in laboratory-decayed wood blocks exposed to *Polyporus versicolor* (PV), *Lenzites trabea* (LT), or *Fomes pini* (FP)

Wood	Fungus	Decay Period		
		3 weeks	6 weeks	12 weeks
<i>Quercus rubra</i> (Red oak)	PV	1.32	1.61	4.07
	LT	2.11	9.79	13.87
<i>Ulmus americana</i> (American elm)	PV	8.33	23.45	32.41
	LT	2.64	5.13	16.33
<i>Acer saccharum</i> (Sugar maple)	PV	6.05	22.81	37.42
	LT	7.08	11.81	17.53
<i>Tilia americana</i> (American basswood)	PV	1.88	7.93	23.69
	LT	9.46	15.81	20.37
<i>Pinus resinosa</i> (Red pine)	FP	0.39	4.68	9.04
	LT	2.43	11.71	22.30
<i>Picea glauca</i> (White spruce)	FP	0.83	2.75	6.40
	LT	1.94	8.79	11.44

All values are averages of 12 replicates for each time period and fungus.

Table 7. Consumption of naturally decayed woodlot wood by soil isopods and diplopods

Wood	Invertebrates							
	<i>Narceus americanus</i>	<i>Pseudopolydesmus serratus</i>	<i>Oxidus gracilis</i>	$\bar{x}$ mg eaten/g/day (millipedes)	<i>Oniscus asellus</i>	<i>Armadillidium vulgare</i>	<i>Armadillidium nasatum</i>	$\bar{x}$ mg eaten/g/day (isopods)
<i>Pinus resinosa</i> (Red pine)	7.41	6.70	3.99	6.03	5.26	4.20	2.18	3.38
<i>Tilia americana</i> ("Dark" American basswood)	4.38	2.90	1.00	2.76	2.89	2.96	2.56	2.80
<i>Tilia americana</i> ("Light" American basswood)	0.55	1.25	5.08	2.29	0.44	1.74	0.81	0.99
<i>Tsuga canadensis</i> ("Dark" Eastern hemlock)	4.03	6.05	0.88	3.65	1.64	1.58	2.81	2.01
<i>Tsuga canadensis</i> ("Light" Eastern hemlock)	2.82	6.38	0.90	3.36	2.28	3.41	2.91	2.86

Data are expressed as mean mg wood/g invertebrate/day for four separate runs.

Table 8. Wood chemical data

Wood	Vanillin Assay (1, 3; 1, 3, 5 phenols)	Folin Assay (total phenols)	4-Amino-phenazone Assay (total phenols)	Water extractable material %	Lignin %	Reducing sugars %
<i>Pinus resinosa</i> (Red pine)	15	144	72	6.30	83.42	12.64
<i>Tilia americana</i> ("Light" American basswood)	8	52	40	13.19	41.89	48.01
<i>Tilia americana</i> ("Dark" American basswood)	9	48	54	13.60	31.22	47.85
<i>Tsuga canadensis</i> ("Dark" Eastern hemlock)	12	112	108	6.71	72.40	19.80
<i>Tsuga canadensis</i> ("Light" Eastern hemlock)	14	120	120	13.73	56.44	43.94

Amount of phenolics present in wood is given in μg of phenolics/10 mg woodlot wood.

Table 9. Rank-ordering of feeding (Table 7) and analytical data (Table 8) with respect to invertebrates and naturally decayed woodlot wood

Wood	Quantity consumed/g isopod/day	Quantity consumed/g diplopod/day	Phenolic content-vanillin procedure	Phenolic content-folin procedure	Phenolic content-4-amino-phenazone procedure	Water soluble content	Lignin content	Reducing sugars content
<i>Pinus resinosa</i> (Red pine)	1	1	1	1	5	5	1	2
<i>Tilia americana</i> ("Dark" American basswood)	4	5	5	5	4	3	4	3
<i>Tilia americana</i> ("Light" American basswood)	5	2	4	4	1	2	5	5
<i>Tsuga canadensis</i> ("Dark" Eastern hemlock)	2	4	2;3	2;3	3	4	2	4
<i>Tsuga canadensis</i> ("Light" Eastern hemlock)	3	3	3;2	3;2	2	1	3	1

4. Discussion

There are scarcely any records on leaf palatability to isopods, EDWARDS (1974) having reported that woodlice prefer *Fraxinus* sp. and *Acer* sp. to *Fagus* sp. With respect to millipedes, a recent review of literature (EDWARDS 1974) revealed three reports in which only 4, 8 and 8 species of leaves, respectively, were tested. In general, these studies showed that *Fagus* and *Quercus* species are scarcely palatable, a finding which is confirmed in the present study. LYFORD (1943) found *Betula lutea* MICH., F. to be second only to *Tilia americana* in an examination of the preferences of *Diploiuulus londonensis* (WOOD) toward 8 leaf species. *B. lutea* and *T. americana* were not examined in the present study, but *B. alleghaniensis*, which was examined, was the first, second or third most preferred leaf to the 8 invertebrates tested (Table 3).

In the present study it is interesting to note that isopods consumed four times more leaf material per gram body weight than millipedes. This statement holds true regardless of whether one compares the top five preferred leaf species, the single most preferred species, or the average of all twenty five leaf species. It is also interesting to note that the reverse situation holds true with respect to wood. For the five wood species together (Table 7), the millipedes consumed 1.5 times as much wood as the the isopods; they consumed an average of 3.61 mg/g/day of the naturally decayed woods, collectively, compared to 2.40 mg/g/day by the isopods.

Our data show there is absolutely no correlation between phenolic content of leaves and feeding preference (Tables 1 and 4; Figs. 2 and 3). Factors other than phenolics, or other factors together with specific kinds of phenolics, should be probed in future studies dealing with the basis or bases for feeding preferences. Similarly, since there is no correlation between water soluble factors and feeding preference, it will be necessary to examine specific chemical components of leaves, or specific physical factors for an insight into leaf preferences.

Failure of the invertebrates to ingest any of the laboratory decayed wood may have been due to their inability to macerate the wood fibers, since the fungi themselves were edible, as is the wood itself when it is sufficiently decayed. Despite the large weight losses

suffered in decaying, the laboratory decayed wood was obviously sturdier than the readily consumed, naturally decayed, woodlot wood. Attesting to the extensive decay that characterized the woodlot wood are the high percentages of lignin (31 to 83) and low percentages of reducing sugars (13 to 48). These values are outside of the normal limits of sound wood. The lignin content in sound wood ranges from 24 to 30 % and 19 to 25 % in softwoods and hardwoods respectively, while the holocellulose content alone, not including other reducing sugars, ranges from 66 to 72 % and 74 to 80 % (KAARIK 1974).

Rank-ordering of the naturally decayed woods on the basis of quantity consumed per unit weight of isopod or millipede and percentage of lignin, reducing sugars, and water soluble extractives is shown in Table 9. Although this ranking is based on values which in some cases are almost identical (e.g., 48 % reducing sugars in dark basswood vs 47.8 % in light basswood), it appears valid to draw a conclusion based upon the apparent trend. In general, the most heavily devoured woods had higher percentages of lignin and phenolics (based on the vanillin and Folin procedures) and lower percentages of carbohydrate. This suggests that, assuming a woody material is ingestible, the animal consumes an amount inversely related to one or more of its readily metabolizable energy sources, such as carbohydrate.

With regard to the percentage of water soluble extractives, there appears to be no correlation to quantity of wood consumed, or, at best, the quantity of water soluble material was inversely related to the quantity of wood consumed (Table 9).

In previous work we have shown that terrestrial isopods are able to degrade substantial quantities of injected benzoic acid (NEUHAUSER et al. 1974), ingested and injected cinnamic and quinic acids, and injected phenol (NEUHAUSER and HARTENSTEIN 1976a). We have also shown that millipedes are able to degrade substantial amounts of ingested cinnamic acid and injected vanillin (unpublished data). Moreover, both taxons oxidized large proportions of $^{14}\text{CH}_3$ from injected p-methoxyphenol (NEUHAUSER and HARTENSTEIN 1976b) and are presumably capable of oxidizing the methyl group of vanillin (unpublished data). Definitive data have now been collected, however, showing that neither taxon is able to depolymerize and degrade lignin (unpublished data).

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6. Summary · Zusammenfassung

(1) The leaf feeding preferences of 4 species of millipedes (diplopods) *Narceus americanus*, *Diplois* sp., *Pseudopolydesmus serratus* and *Apheloria coriacea*, and 4 species of isopods, *Oniscus asellus*, *Armadillidium vulgare*, *Armadillidium nasatum*, and *Porcellio scaber* were determined through an analysis of 800 observations of feeding on 25 species of leaves.

(2) Four of the 25 species of leaves (*Acer negundo*, *Ailanthus altissima*, *Betula alleghaniensis* and *Salix nigra*) were favored by each of the invertebrate species, while species of Fagaceae were least preferred, less so than coniferous needles. Isopods consumed a greater quantity of leaves per unit body weight ($\bar{X}$ 14.62 mg/g/day) than millipedes ($\bar{X}$ 3.31 mg/g/day) based upon the top five preferred species of leaves.

(3) Neither the phenolic content nor the water extractable content of the leaves was related to leaf palatability.

(4) Upwards to about 50 % and 30 % of the phenolic content of leaves disappeared upon being consumed by an isopod, *O. asellus* and a diplopod, *P. serratus*, respectively.

(5) Neither isopods nor millipedes were able to ingest laboratory decayed wood, wood which was decayed by monocultured fungal species for specified periods of time. Both invertebrate taxa readily consumed heavily decayed wood from a woodlot, the diplopods consuming 1.5 times as much as the isopods.

Phenolgehalt und Freßbarkeit von Blättern und Holz für bodenlebende Isopoden und Diplopoden

1. Durch Analyse von 800 Beobachtungen des Fraßes an 25 Blattarten wurde die Nahrungswahl von 4 Diplopoden- (*Narceus americanus*, *Diploiuulus* sp., *Pseudopolydesmus serratus* und *Apheloria coriacea*) und 4 Isopoden-Arten (*Oniscus asellus*, *Armadillidium vulgare*, *A. nasatum* und *Porcellio scaber*) bestimmt.
2. Vier der 25 Blattarten (*Acer negundo*, *Ailanthus altissima*, *Betula alleghaniensis* und *Salix nigra*) wurden von jeder der genannten Wirbellosen-Arten bevorzugt, während Arten von Fagaceen am wenigsten bevorzugt wurden, weniger als Koniferennadeln. Isopoden konsumierten (auf das Körpergewicht bezogen) eine größere Menge der 5 am meisten bevorzugten Blattarten ($\bar{X} = 14,62$ mg/g/d) als Diplopoden ($\bar{X} = 3,31$ mg/g/d).
3. Weder der Phenolgehalt noch der Gehalt an wasserlöslichen Substanzen stand zur Geschmacksbevorzugung in Beziehung.
4. Der Isopode *Oniscus asellus* und der Diplopode *Pseudopolydesmus serratus* haben Blätter mit einem geringeren Phenolgehalt von etwa 50 und 30 % nicht mehr angenommen.
5. Weder Isopoden noch Diplopoden waren imstande, Holz aufzunehmen, das durch Monokulturen von Pilzarten im Laboratorium während bestimmter Zeiten zersetzt wurde. Beide Wirbellosen-Taxa konsumierten bereitwillig stark zersetztes Holz aus einem Waldstück; die Diplopoden konsumierten 1,5mal mehr als die Isopoden.

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